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Microhabitat Use by Macroinvertebrates in Barataria Bay, Louisiana

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MICROHABITAT USE BY MACROINVERTEBRATES
IN BARATARIA BAY, LOUISIANA

A Thesis

Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Master of Science

in

The Department of Oceanography and Coastal Sciences

by
William H.F. Hayden
B.S., University of Southern California, 1981
August 1994

MANUSCRIPT THESES

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ABSTRACT

A drop sampler was used to collect macroinvertebrates along transects in open and closed marshes within the Barataria Basin. Three-hundred-seventy-seven samples, covering 448 m², were collected between August 1988 and September 1989. Sampling focused along the marsh edge where open water and flooded *Spartina* meet, covering a broad range of environmental conditions including different stem densities, distances to the marsh edge, and water depths. Other variables measured included water temperature, velocity, dissolved oxygen, salinity, turbidity, substrate, and marsh vegetation. Of the ten most frequently-occurring macroinvertebrates, three were transients (*Callinectes sapidus*, *C. similis*, and *Penaeus aztecus*), and seven were residents (*Mysidopsis* spp., *Palaemonetes* spp., *Clibanarius vittatus*, *Eurypanopeus depressus*, *Ampilescia vadorum*, *Gammarus mucronatus*, and *Neanthes succinea*).

A size-frequency analysis showed that most seasonal abundance peaks were recruitment peaks. *P. aztecus*, *G. mucronatus*, *N. succinea*, and *Mysidopsis* showed spring recruitment. *C. sapidus* and *E. depressus* showed summer, and *C. similis* showed fall recruitment peaks. *Palaemonetes* and *A. vadorum* showed winter recruitment. *C. vittatus* showed two peaks, winter and summer.

Factor analysis described three well-defined axes that explained 52.3% of the variance. These were seasonal (temperature and dissolved oxygen), microspatial (depth, distance, and stem density), and macrospatial (salinity). In univariate analyses, differential patterns of microhabitat use were significant among several species. Among residents, *Palaemonetes* was different from *Mysidopsis* in temperature, depth, and stem density. Among the transients, *Penaeus aztecus* and the two *Callinectes* species differed in temperature, and the *Callinectes* species differed in stem density, salinity, and turbidity. There were generally more differences among transients than among residents.

A tethering experiment was also conducted to examine differential day and night survival rates in the marsh edge. This was a preliminary examination of predation as an explanation for microhabitat selection. Aside from some confounding factors, analyses showed that some daytime survival rates were significantly lower.

CHAPTER 1

INTRODUCTION TO THE STUDY

The purpose of this study was to analyze environmental factors that influence the distribution and abundance of fishes and macroinvertebrates in the marsh-edge ecotone. To realize this purpose several questions were addressed. First, how are the microhabitats used by important species characterized, and how does microhabitats use differ between species? Second, what are the seasonal patterns of size-frequency distribution? And finally, what are the major environmental conditions that influence community structure? Chapter Two is an examination of these questions, focusing on macroinvertebrate distribution and abundance in the marsh-edge ecotone. In Chapter Three, the results of a preliminary experiment that examined day versus night survival in the marsh-edge ecotone are examined. The field work was conducted in conjunction with a study of microhabitat use by fishes and two species of *Callinectes*. The fishes have already been examined in other studies (Rakocinski et al. 1992, Baltz et al. 1993), and *C. sapidus* and *C. similis* were compared in a study by Gibson (1991).

Community structure of marsh-edge fishes was examined in relation to environmental gradients in Rakocinski et al. (1992). They described patterns in the community structure and identified large-scale temporal and spatial changes in the community structure of fishes that coincide with environmental gradients. Finally, they recognized that

environmental gradients act at different times and on different scales, and that nested within large-scale gradients are local environmental gradients that coincide with changes in community structure.

In an analysis of microhabitat use by marsh-edge fishes, Baltz et al. (1993) showed significant differences for selected fishes which reflected the ephemeral duration of early life history stages, the existence of ontogenetic microhabitat shifts, and the complex dimensionality of the system. They also confirmed the importance of the marsh-edge ecotone as a nursery for many estuarine-dependent fishes.

This study is a step toward a broader understanding that will result from comparison of microhabitat use by fishes and by macroinvertebrates. Such a comparison will show a better linkage between the descriptive field study of Chapter Two and the experimental analysis of predation in Chapter Three. The study of what microhabitats are selected leads directly to the question of what factors influence their selection. Testing for links between the fish and invertebrate communities could lead to the discovery of patterns that might indicate important interactions between species. The study in Chapter Three was an initial effort to look at predation as an influence on microhabitat selection in the marsh-edge ecotone. The experimental technique of chronographic tethering,

originally developed by Minello (1993), was used to estimate and compare survival time of fish at the marsh edge during the day and at night. Emigration from vegetated habitats when it occurs at all should happen at night to minimize predation risk (Virnstein and Curran 1986). This hypothesis was tested by tethering fish over unvegetated substrates at the marsh edge. The predation experiment was conducted during the day and at night to test whether daytime and nighttime survival rates were significantly different.

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CHAPTER 2

MICROHABITAT UTILIZATION BY MACROINVERTEBRATES IN BARATARIA BAY, LOUISIANA

Introduction

The quality and quantity of nursery habitat may control the population size of many estuarine-dependent organisms. Therefore, knowledge of the range of environmental tolerance and optimum conditions that facilitate growth and survival of important species and their common prey is critical to habitat management. The loss of wetlands in Louisiana is a major threat to many fisheries of the northern Gulf of Mexico. Coastal wetlands in Louisiana directly support 28% of the national fisheries landings (Turner 1990). Many of the fishery species are estuarine dependent which means that coastal wetland habitat conservation can be equated to fishery management for several species, especially the commercially important penaeid shrimp (Turner 1992).

The concept of estuarine dependence implies that an estuary is important for some portion of the life cycle of an organism, often as a nursery area (Day et al. 1989). The presence of large numbers of eggs, larvae, or post-larvae within an estuary, combined with their relatively lower abundance in the other coastal environments usually defines an estuary as a nursery ground (Pearcy and Myers 1974). This has been shown to be true for brown shrimp (*Penaeus aztecus*) (Larson et al. 1989), white shrimp (*P. setiferus*) (Muncy 1984), blue crab (*Callinectes sapidus*)

(Thomas et al. 1990), and many other commercial fishery species. The juveniles of many fishery species use flooded *Spartina* marshes extensively along the Gulf Coast in general (Zimmerman et al. 1990) and in Barataria Bay specifically (Rakocinski et al. 1992, Baltz et al. 1993).

The question as to why estuarine environments, especially the marsh-edge ecotone, are important nursery grounds has long been a matter of debate. One paradigm cited as a causative factor is reduced predation due to shallowness (Ruiz et al. 1993), turbidity (Cyrus and Blaber 1992), or aquatic vegetation. This hypothesis has been supported in a number of field experiments, especially the question of vegetation or structural effects (Heck and Thomas 1981, Minello and Zimmerman 1983a, 1983b, Werner et al. 1983, Zimmerman and Minello 1984, Knieb 1987, Minello et al. 1989, Savino and Stein 1989, Lubbers et al. 1990, Cyrus and Blaber 1992, Orth 1992), and questioned in some others (Knieb 1984, Bell and Westoby 1986). Another paradigm is that the organisms are attracted to the presence of greater prey density associated with aquatic vegetation (Gerking 1962, Gleason and Wellington 1988, Gotceitas 1990, Gotceitas and Colgan 1990, Rozas and LaSalle 1990, Minello and Zimmerman 1991). Some researchers have shown that whichever paradigm is the cause for habitat choice, actual habitat selection is based on physicochemical characteristics (Bell and Westoby 1986).

Whichever paradigm is correct, it is important for estuarine resource managers to know which environmental variables are important in controlling the distribution and abundance of particular organisms in nursery habitat. For the macroinvertebrates using the marsh-edge ecotone within the lower Barataria Basin, several analyses were conducted. The purpose of these analyses was to characterize microhabitat use patterns of important species, to determine their seasonal abundance patterns, and to discover what environmental conditions influenced the overall community structure.

Most macroinvertebrate species examined in this study showed seasonal peaks of abundance, and size-frequency analyses indicated that the peaks were due to recruitment of smaller size classes into the marsh-edge ecotone. In a factor analysis, the major axes that influenced community structure for these organisms were seasonal variables including temperature and dissolved oxygen, a microspatial gradient including depth, distance to the marsh edge, and density of *Spartina* stems, and a spatial macrogradient that reflected variation in salinity.

Study Area

The Barataria Basin of Louisiana lies between the levees of the Mississippi River and Bayou Lafourche. It stretches 110 km inland from the Gulf of Mexico (Fig. 1). Samples for this study were collected in the lower basin, within Barataria and Caminada bays. This region is characterized as *Spartina alterniflora* salt marshes, which cover approximately 145,000 ha (Conner and Day 1987).

Erosion of marsh lands is a major problem in the Barataria Basin (Baumann 1987). Since the completion of the river levees more than 50 years ago, there has been little direct river flow into the basin. Currently, precipitation is the main source of freshwater input, averaging 160 cm per year. Salinities in the basin are influenced primarily by tidal flux, precipitation, and prevailing winds. In the lower estuary, salinity ranges between 4 and 28 ppt with both spatial and seasonal variability. The hydrography of the basin is also influenced by tidal flux and prevailing winds. Summer is the season with the most stable hydrographic conditions because of less variable weather patterns (Baumann 1987). The microtidal system is generally less than 2 m deep, and it has a mean tidal range of 0.32 m.

Within the protected shores of the basin, there are extensive tidal flats and saltgrass marshes. The substrate

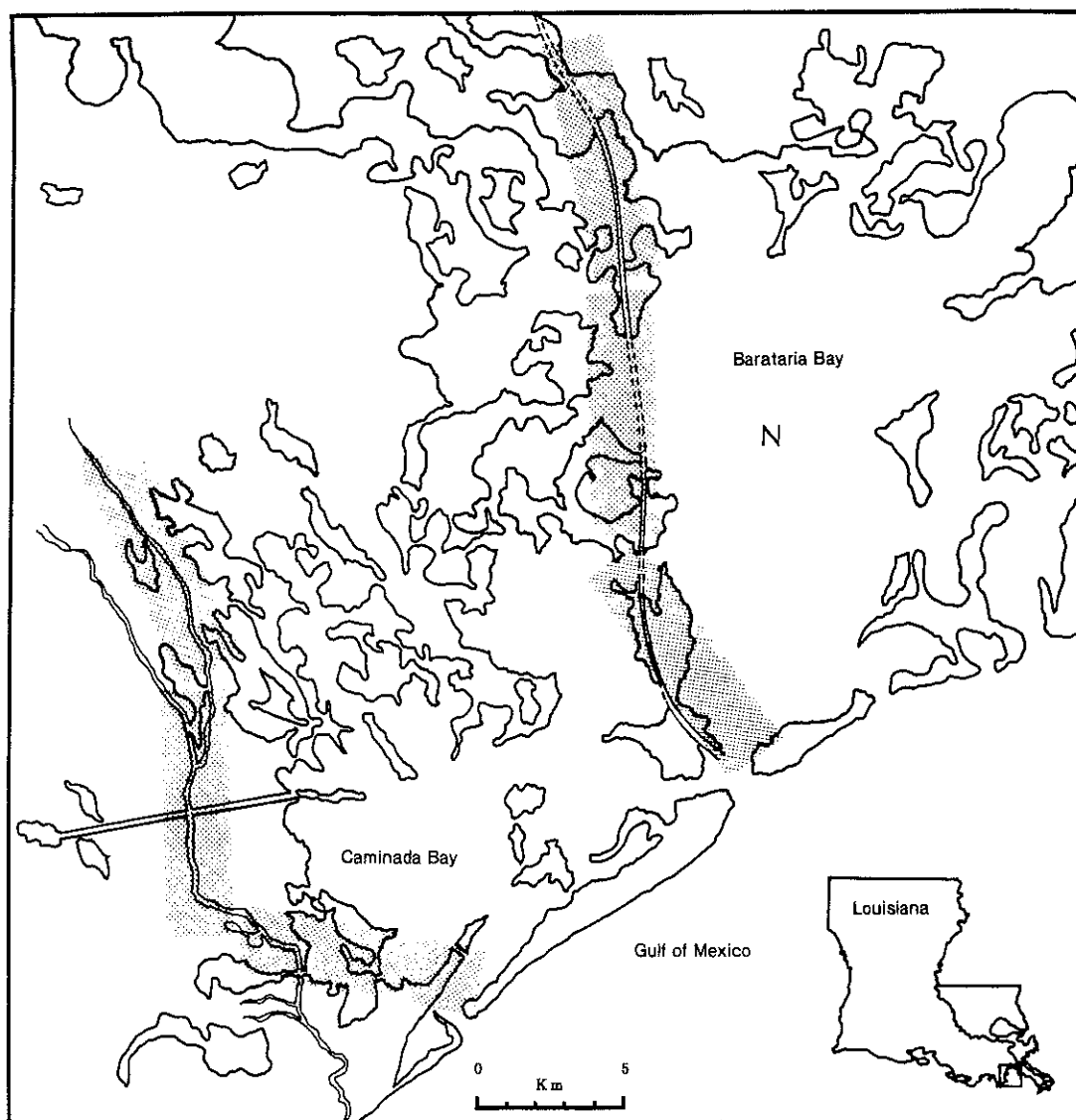


Figure 1. Map of the lower Barataria Basin showing the two sampling transects.

is mostly fine grained inorganic sediment (mud) and organic detritus; however, sand and clay are found in the lower reaches of the study area. The marsh vegetation is dominated by *Spartina alterniflora* (salt marsh cordgrass), but also includes *Juncus roemerianus* (black rush), *Distichlis spicata* (saltgrass), *Batis maritima* (saltwort), *Salicornia virginica* (glasswort), and *Avicennia germinans* (black mangrove). In upper reaches of the salt marsh, *Spartina alterniflora* grades into the brackish-water species, *Spartina patens* (salt meadow cordgrass).

Materials and Methods

Quantitative samples of macroinvertebrates and fishes were collected along two transects within the lower portion of the Barataria Basin that run from the Gulf of Mexico inland for approximately 25 km (Fig. 1). One transect was located along the Barataria Waterway which transits the open sections of Barataria Bay. This transect can be characterized as open marsh. The other transect, located in the marshes west of Caminada Bay, can be characterized as closed marsh. To evaluate organism responses along the salinity gradient, sampling effort was stratified among the upper, middle, and lower reaches of each transect.

A drop sampler approach (Zimmerman et al. 1984) was used to collect marsh-edge invertebrates. The samples were

taken using a 1.23 m diameter cylindrical fiberglass drop sampler (1.188 m² in area). The sampler was suspended 3 m forward of the bow of a small boat and about 0.5 m above the water. A release mechanism allowed us to drop the sampler on a selected site. This sampling method retained all sizes of fishes and invertebrates, and nearly complete sampling of individuals in the enclosed area provided an accurate estimate of densities for all but the burrowing species (Zimmerman et al. 1984). As the sampling area was small and homogeneous, microhabitat information was obtained for all taxa and size classes in each sample.

Microhabitat use refers to fine-scale use of space at sites occupied by individuals, and the ultimate microhabitat is the space occupied by the individual (Hulbert 1981). Sites may be characterized by measuring physicochemical variables (e.g., depth, velocity, temperature, salinity) that describe environmental conditions (Baltz 1990). Many individual measurements of this kind allow the building of a picture of the pattern of use by species or life history stages (i.e., the pattern of population response to environmental gradients). In this study it would have been impractical to characterize the ultimate microhabitats for all of the organisms within the sampler; therefore, the physicochemical measurements at each sample site were taken either in or within a meter of the sampler itself. Habitat is defined from an

autecological viewpoint (i.e., habitat is the range of environments or environmental conditions used by a population or life-history stage). The study is focused in the marsh-edge ecotone, which is the transition zone between flooded *Spartina alterniflora* marsh and open water (Baltz et al. 1993).

A total of 377 samples, covering 448 m² were collected by monthly sampling that began in August 1988 and ended in September 1989. Whenever possible, sampling was conducted in all three reaches of a transect during each sampling trip and transects were alternated each trip. Samples were taken from a broad range of environmental conditions along the marsh edge, including different stem densities (ranging from 0 to 320 stems m⁻²), distances to the marsh edge (ranging from 0 to 15 m), and water depths (ranging from 1 to 88 cm). One or more samples within each reach usually included grass stems (25.7% of 377 samples), but access depended on the tidal height. Samples containing stems were either on the flooded marsh surface or at the interface of the marsh and open water. Approximately a third of the samples (35.6%) were in open water (containing no grass stems) within 1 m of the marsh edge, and the remainder (38.7%) were in open water more than 1 m from the marsh edge.

Several environmental variables were measured at each sample site, including the minimum and maximum depths within the sampler (from which a midrange depth was calculated and used in all analyses) and the minimum distance to the marsh edge. The dominant marsh vegetation adjacent to each sample site was recorded, and the dominant and subdominant substrates within the sampler were characterized. The substrates at each sampling site were coded on an ordinal scale of particle size as 1: fines (clay and silt), 2: sand, 3: organic detritus, and 4: shell or shell fragments. When emergent grasses were present in the sampler, a count was made of the total number of stems. Other environmental variables measured included current velocity (cm s^{-1}), turbidity (NTU), salinity (ppt.), water temperature ($^{\circ}\text{C}$), and dissolved oxygen (DO mg l^{-1}). The equipment used for these measurements included, an AO temperature compensated refractometer, YSI model 33 S-C-T and model 57 oxygen meters, a Monitek model 21 PE portable nephelometer, and a Montedoro-Whitney PVM-2 current meter.

After the sampler was deployed and firmly seated the environmental variables were measured and a suspension of 100 cc of powdered rotenone (5%) and marsh water was introduced into the sampler. Organisms that swam to the surface were removed with dip nets and preserved in 95% ethanol. After thoroughly dip-netting, the remaining water was pumped through a 333-micrometer plankton net to retain

organisms. Any remaining organisms were removed from the substrate surface by hand or with dip nets. Organisms living within the substrate were taken when they rose to the surface layer, or when the intake hose accidentally made contact with the substrate. Consequently, many burrowing species may not have been representatively sampled by this method.

Several keys were used for macroinvertebrate identification, including Heard (1979), Felder (1973), Hopkins and Valentine (1987), and an unpublished mysid key provided by Richard Heard (Gulf Coast Research Laboratory, Ocean Springs, MS).

For the ten most frequently occurring invertebrates, resident species were defined as those for which all life-history stages are found in the Barataria Basin. Transient species were defined as those for which at least one life-history stage is not found in the estuary. Essentially, this transient group consisted of species that move offshore to spawn (*Penaeus aztecus* and *Callinectes spp.*)

Although several species of mysid and grass shrimp were present, for the analyses, all mysids and grass shrimps were grouped generically. In both cases these groups were dominated by a single species that made up over 90% of that group.

Mysids (*Mysidopsis spp.*) were counted individually when scarce. When samples of mysids were too large to

count, a volumetric estimate of the number of individuals was made using five samples from a Henson-Stemple pipette. Twenty randomly selected samples, from all samples which contained mysids, were examined in detail and found to contain two species *M. almyra* (95.3%) and *M. bahia* (4.7%). Other species may have been present; however, these would represent a small fraction of the total mysids taken.

Grass shrimp (*Palaemonetes* spp.) were always counted individually; however, difficulties existed in identifying them to the species level. Twenty randomly selected samples from all samples that contained grass shrimp were also examined in detail and were found to contain two species, *Palaemonetes pugio* (92.1%) and *P. vulgaris* (7.9%). Other species may have been present; however, these would represent a fraction of the total *Palaemonetes* spp. taken.

A third taxon, *Callinectes* unk., included two individual portunid crabs that could not be identified to the species level due to damage or other difficulties, but were certainly not *C. sapidus* or *C. similis*. Other possible species from the northern Gulf of Mexico include: *C. exasperatus*, *C. marginatus*, *C. ornatus*, and *C. rathbunae* (Felder 1973).

Patterns of microhabitat use and environmental variation were examined among seasons and among the ten most frequently occurring macroinvertebrates. Seasonal characterization of the marsh-edge environment was examined

with a one-way analysis of variance (ANOVA) on each of nine variables using the general linear model (GLM) procedure in SAS (SAS Institute 1985). To interpret the seasonality of environmental variables, the seasonal means were tested using Scheffe's multiple range comparison test at an α level of 0.05. Patterns of microhabitat use for each individual environmental variable by the ten most frequently occurring species were also compared with GLM ANOVAs and Scheffe's method, within resident and transient species groups.

Seasonal and size-frequency analyses of mean monthly densities were conducted to identify seasonal recruitment patterns for seven of the ten most frequently occurring species. Two amphipod species (*Gammarus mucronatus* and *Ampileasca vadorum*) were excluded from the size-frequency analysis as was the polychaete *Neanthes succinea*, because it was felt that the size distributions may not have been well characterized. Size measurement, which was conducted to 1 mm, would have shown little variance for the amphipods. The polychaetes, most often taken in sediment plugs through the pump, were often damaged to the point that measurement was impractical. These species were still included in the other analyses because they were among the most frequently occurring species, and although they were infauna, their minimum abundances were estimated by the sampling procedure.

Variations in the patterns of microhabitat use were examined in a factor analysis of eight environmental variables for the ten most frequently occurring macro-invertebrates. Substrate was excluded from the analysis as it was the only ordinal variable among several continuous variables. The analysis was based on the untransformed microhabitat variables using the varimax rotation method. It was run using a factor analysis program (PROC FACTOR) of SAS (SAS Institute 1985). The varimax rotation maximizes the loading of each environmental variable on one factor while reducing it on all others. This method afforded the easiest interpretation of the factor loadings.

A factor analysis on the physicochemical data from a microhabitat-scale study generates a multidimensional set of environmental axes that reflect variation in seasonality, macrogradients, and microspatial gradients. Species centroids and standard errors were calculated from the factor scores of samples containing each species after weighing by the number of individuals present. They were then plotted onto the three primary environmental axes (excluding Factor Four) using a three-dimensional graphics procedure (PROC G3D) from SAS (SAS Institute 1985). This type of plot gives a picture of the population response patterns in three-dimensional factor space. Moving along one or more axes of environmental space, one sees changing associations of species as changes in community structure.

When microhabitat use data are analyzed by looking at a factor analysis of the environmental variables, certain variables are going to introduce a seasonal effect on the gradient axes. It is inevitable in this kind of analysis that the seasonal effects will weigh heavily for any organism with seasonal recruitment peaks. In addition to seasonality, patterns of use are complicated by ontogenetic shifts in the environmental or physiological requirements of life-history stages.

Results

In 377 samples obtained between August 1988 and September 1989, we collected 38 invertebrate species and 39,894 individuals (Table 1). The ten most frequently occurring invertebrates, comprising 96.3% of all individuals, were chosen for most of the following analyses. The most common taxon was the mysid group, *Mysidopsis spp.*, which numerically represented 65.6% of the macroinvertebrates caught. The grass shrimp, *Palaemonetes spp.*, as the second most numerically common taxon, represented 14.7% of the total. *Gammarus mucronatus*, an amphipod, was the most common taxon identified to species, at 5.1% of the numerical total. *Callinectes sapidus*, the blue crab, ranked fourth numerically at 3%, but ranked first in frequency of occurrence (66.8% of all samples).

Table 1. List of the 38 macroinvertebrate species ranked by numerical abundance in 377 drop samples collected in the Barataria Basin, Louisiana, between August 1988 and September 1989. Abbreviations are given for the ten most frequently occurring species and are used in Figure 9.

Species	Code	Abundance		Occurrence	
		Number	Portion	Frequency	Portion
<i>Mysidopsis</i> <i>spp.</i> ¹	Mspp	26075	0.654	233	0.618
<i>Palaemonetes</i> <i>spp.</i> ²	Pspp	5848	0.147	241	0.639
<i>Gammarus</i> <i>mucronatus</i>	Gm	2019	0.051	105	0.279
<i>Ampileasca</i> <i>vadorum</i>	Av	1666	0.042	83	0.22
<i>Callinectes</i> <i>sapidus</i>	Csap	1211	0.03	252	0.668
<i>Penaeus</i> <i>aztecus</i>	Pa	471	0.012	115	0.305
<i>Eurypanopeus</i> <i>depressus</i>	Ed	336	0.008	78	0.207
<i>Corophium</i> <i>louisianum</i>		322	0.008	14	0.037
<i>Neanthes</i> <i>succinea</i>	Ns	304	0.008	95	0.215
<i>Grandidierella</i> <i>bonnieroides</i>		286	0.007	39	0.103
<i>Callinectes</i> <i>similis</i>	Csim	235	0.006	82	0.218
<i>Hargeria</i> <i>rapax</i>		223	0.006	6	0.016
<i>Corophium</i> <i>tuberculatum</i>		208	0.005	44	0.117
<i>Clibanarius</i> <i>vittatus</i>	Cv	204	0.005	94	0.249
<i>Penaeus</i> <i>setiferus</i>		107	0.003	44	0.117
<i>Alpheus</i> <i>floridanus</i>		100	0.003	32	0.085
(table con'd.)					

<i>Cyrenoida</i> <i>floridana</i>	74	0.002	33	0.088
<i>Melita</i> <i>longisetosa</i>	57	0.001	10	0.027
<i>Nassarius</i> <i>vibex</i>	45	0.001	22	0.058
<i>Streblospio</i> <i>benedicti</i>	26	0.001	2	0.005
<i>Chone</i> <i>sp.</i>	17	<0.001	7	0.019
<i>Panopeus</i> <i>herbstii</i>	16	<0.001	3	0.008
<i>Geukensia</i> <i>demissa</i>	14	<0.001	9	0.024
<i>Cassidinea</i> <i>ovalis</i>	5	<0.001	5	0.013
<i>Callinectes</i> <i>similis</i>	4	<0.001	4	0.011
<i>Alpheus</i> <i>normanii</i>	4	<0.001	4	0.011
<i>Sphaeroma</i> <i>tenebrans</i>	4	<0.001	3	0.008
<i>Edotea</i> <i>triloba</i>	2	<0.001	2	0.005
<i>Detracia</i> <i>floridana</i>	2	<0.001	2	0.005
<i>Callinectes</i> <i>unk.</i> ³	2	<0.001	2	0.005
<i>Scoloplos</i> <i>fragilis</i>	2	<0.001	1	0.003
<i>Ampilesca</i> <i>abdit</i>	1	<0.001	1	0.003
<i>Rhithropanopeus</i> <i>harrisii</i>	1	<0.001	1	0.003
<i>Laeonerieis</i> <i>culveri</i>	1	<0.001	1	0.003
crab zoea	1	<0.001	1	0.003

(table con'd.)

juvenile	1	<0.001	1	0.003
cymothoid				
isopod				

Total	39894
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Invertebrates

¹ *Mysidopsis* spp. consisted of *M. almyra* (95.3%), and *M. bahia* (4.7%) in 20 random samples from the collection containing *Mysidopsis*.

² *Palaemonetes* spp. consisted of *P. pugio* (92.1%), *P. vulgaris* (7.9%) in 20 random samples from the collection containing *Palaemonetes*.

³ *Callinectes* unk. consisted of unidentified crabs of this genus other than *C. sapidus* or *C. similis*.

Of the ten most frequently occurring taxa, *C. sapidus* and *Penaeus aztecus*, the brown shrimp, were the only commercial species. Other taxa included mud crabs, several species of amphipod, polychaete worms, mud snails, hermit crabs, and some small bivalves.

In univariate analyses of environmental variables measured in association with the 377 samples, environmental conditions changed seasonally in the marsh-edge ecotone (Table 2). Temperature and dissolved oxygen showed significant differences among seasons. Mean temperature had an increasing trend from the winter months (December-February) through the summer (June-August), then decreased in fall (September-November). Mean dissolved oxygen, which was negatively correlated with temperature, showed a decreasing trend through the year. Mean salinity showed a significant decrease over the spring and summer months. Mean water velocity showed a significant decrease in fall. Turbidity showed a significant increase in the spring and summer months.

Two significant results of the seasonal analyses of environmental variables were the greater mean distance from the marsh edge and the lower mean stem densities found in winter (Table 2). The variance of stem density was high in all seasons due to the large number of zeros included (>60% of 377 samples), and few stems were flooded during the winter. The lower mean stem density in winter was due

Table 2. Seasonal means and standard deviations for nine environmental variables at drop-sampling sites in the Barataria Basin, Louisiana. N is the number of independent samples. The letters, read horizontally, show significant differences among seasons (Scheffe's test $p < 0.05$).

	Dec-Feb	Mar-May	Jun-Aug	Sep-Nov	Annual Mean
N	25	136	151	65	377
Temperature (°C)	15.8±1.22A	25.0±4.03B	29.9±1.65C	26.9±5.07D	27.5
D.O. (mg l ⁻¹)	8.6±0.44A	7.5±1.04B	7.1±1.34C	6.4±1.49D	7.2
Median Depth (cm)	35.6±14.17	39.3±12.91	41.7±13.99	39.4±14.88	40.4
Distance from marsh edge (m)	2.6±2.02A	1.4±1.87B	1.6±1.41AB	1.6±1.80AB	1.5
Stem Density (m ⁻²)	0.3±1.68	7.6±24.99	5.4±15.64	15.1±46.10	7.1
Salinity (o/oo)	21.4±3.22A	16.2±2.47B	15.8±4.82B	19.7±4.72A	16.4
Velocity (cm s ⁻¹)	3.5±2.74AB	3.6±4.58A	3.2±3.13A	1.4±1.28B	3.2
Turbidity (NTU)	9.3±5.76A	21.9±15.32B	18.2±8.20B	11.6±9.58A	19
Substrate	2.0±0.96AB	1.9±0.96AB	1.6±0.90A	2.0±0.96B	1.8

primarily to low-water events resulting from northerly winds. During the winter months, northerly winds often force water out of the estuary, reducing the water depth and exposing marsh-edge mudflats. Despite this, I believe that our sampling adequately characterized common macroinvertebrates that use the marsh-edge ecotone.

Species densities ranged from 1 to 2,138 individuals per square meter (Table 3), and most of the common species showed a seasonal peak within the marsh-edge ecotone. Among the ten frequently occurring taxa, one species showed a winter peak in abundance, two graded from winter into spring, five showed spring abundance peaks, and two had peaks of abundance in the summer.

Of the resident taxa, *Mysidopsis* spp. and *Ampilescavadorum*, an amphipod, showed significantly higher mean densities in the spring months (March-May). This can be inferred to indicate seasonal recruitment. *Palaemonetes* spp. showed a recruitment pattern that began in fall (September-November) and peaked in winter (December-February). Of the transient taxa, only *Callinectes sapidus* showed a clear peak in abundance, indicating a summer recruitment.

In the seasonal size-frequency analysis for the most common transient taxa, *Penaeus aztecus* showed a nearly complete absence in winter followed by a sudden, broad-ranging increase of size classes in spring (Fig. 2). There

Table 3. Seasonal mean and maximum densities at capture sites for selected invertebrates in the marsh edge of the Barataria Basin, Louisiana. Numbers are mean density (number m⁻²) \pm 1 SE (maximum density). The letters, read horizontally, show significant species differences (Scheffe's test, $p < 0.05$) between seasons.

Species	Dec-Feb	Mar-May	Jun-Aug	Sep-Nov
Resident				
<i>Palaeomonetes</i>	55.8 \pm 17.7 (331)A	17.3 \pm 2.16 (106)B	10.0 \pm 1.58 (61)B	24.0 \pm 6.50 (139)B
<i>spp.</i>				
<i>Mysidopsis</i>	15.4 \pm 4.29 (40)AB	168.4 \pm 35.4 (2138)A	66.5 \pm 6.5 (438)B	15.1 \pm 2.09 (40)B
<i>spp.</i>				
<i>Gammarus</i>	5.2 \pm 3.19 (27)	22.4 \pm 5.11 (320)	4.2 \pm 0.95 (17)	7.9 \pm 9.07 (28)
<i>mucronatus</i>				
<i>Clibanarius</i>	2.7 \pm 1.11 (6)	2.2 \pm 0.32 (8)	1.2 \pm 0.17 (4)	1.8 \pm 0.31 (5)
<i>vittatus</i>				
<i>Neanthes</i>	2.5 \pm 0.85 (10)	4.0 \pm 0.85 (26)	1.5 \pm 0.14 (3)	1.5 \pm 0.25 (3)
<i>succinea</i>				
<i>Ampilesc</i>	23.7 \pm 6.88 (78)AB	22.5 \pm 3.64 (103)A	11.2 \pm 1.23 (29)B	2.9 \pm 1.26 (4)AB
<i>vadorum</i>				
<i>Eurypanopeus</i>	1.1 \pm 0.21 (2)	2.0 \pm 0.34 (10)	6.4 \pm 1.82 (31)	1.8 \pm 0.28 (3)
<i>depressus</i>				
(table con'd.)				

Transient					
<i>Callinectes</i>	3.7±0.62 (13)AB	2.3±0.22 (11)A	5.8±0.58 (32)B	3.4±0.40 (9)A	
<i>sapidus</i>					
<i>Penaeus</i>	0.8 (1)	4.3±0.52 (17)	2.6±0.48 (14)	1.8±0.34 (3)	
<i>aztecus</i>					
<i>Callinectes</i>	1.3±0.28 (3)	2.8±0.33 (10)	0 (0)	2.2±0.71 (14)	
<i>similis</i>					

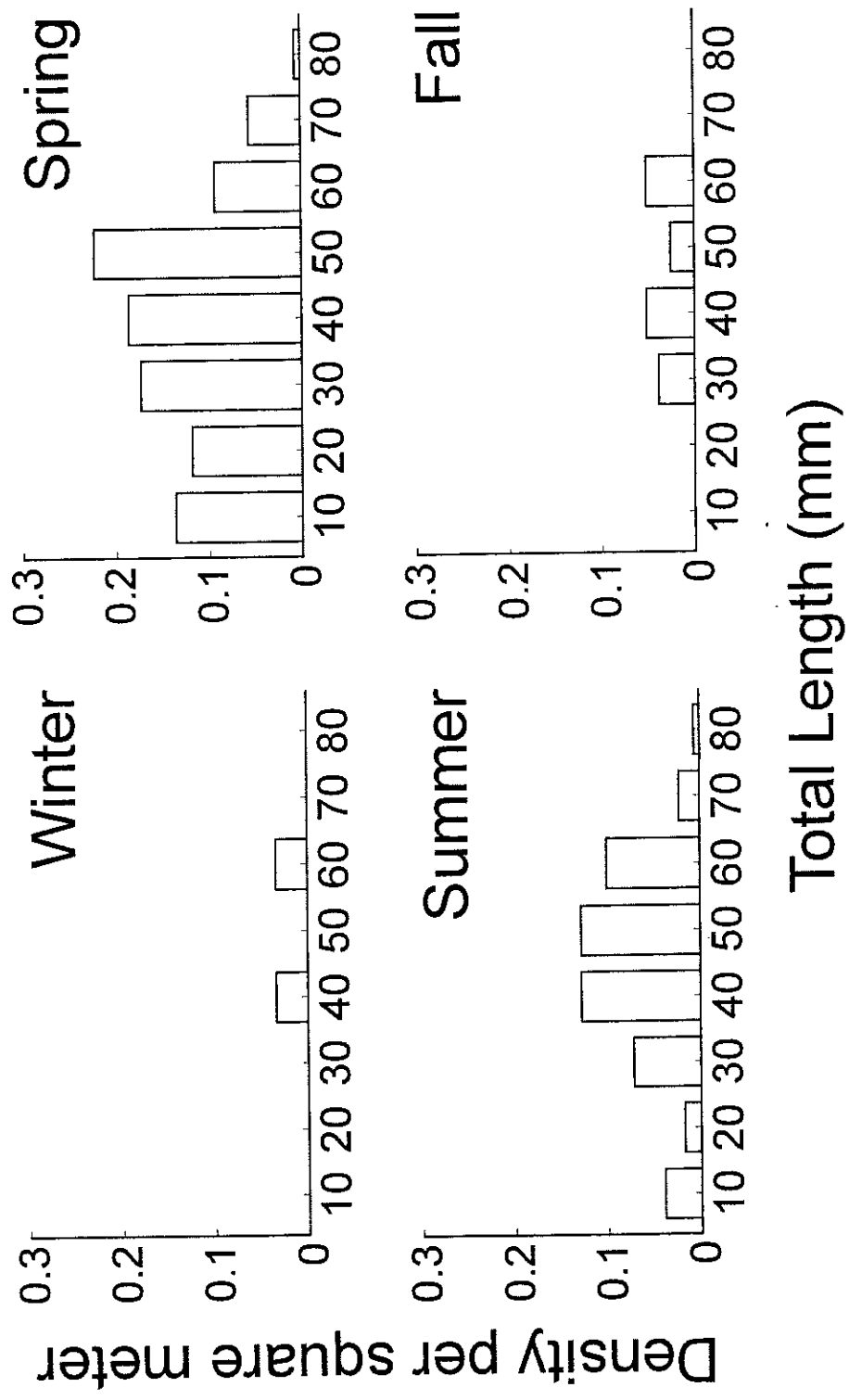


Figure 2. Size-frequency versus mean density per square meter by season for *Penaeus aztecus*.

was a reduction in the density of smaller size classes through summer, presumably indicating growth. This was followed by a reduction in density of both the smallest and the largest size classes from spring through winter. The loss of larger individuals may reflect ontogenetic movements and/or fishing mortality.

The other two transient species were both portunid crabs. *Callinectes sapidus* showed a distinct recruitment peak in the 4 mm CW size interval in the summer (Fig. 3). There was a large reduction in this peak in the fall as individuals grew. There was growth into the larger size classes in the winter followed by an overall reduction of density of all size classes in spring that may indicate movement into deeper waters within the estuary or offshore. *Callinectes similis*, the lesser blue crab, showed the most unusual seasonal pattern of size-frequency distribution (Fig. 4), in that it was not observed in the summer (Fig. 4, Table 3). The density of *C. similis* was generally one order of magnitude lower than that of *C. sapidus*. During summer *C. similis* may have moved into deeper waters or offshore for spawning, because an apparent recruitment peak occurred in the fall. Two equal peaks of abundance for the smallest size classes occurred in the fall and the winter.

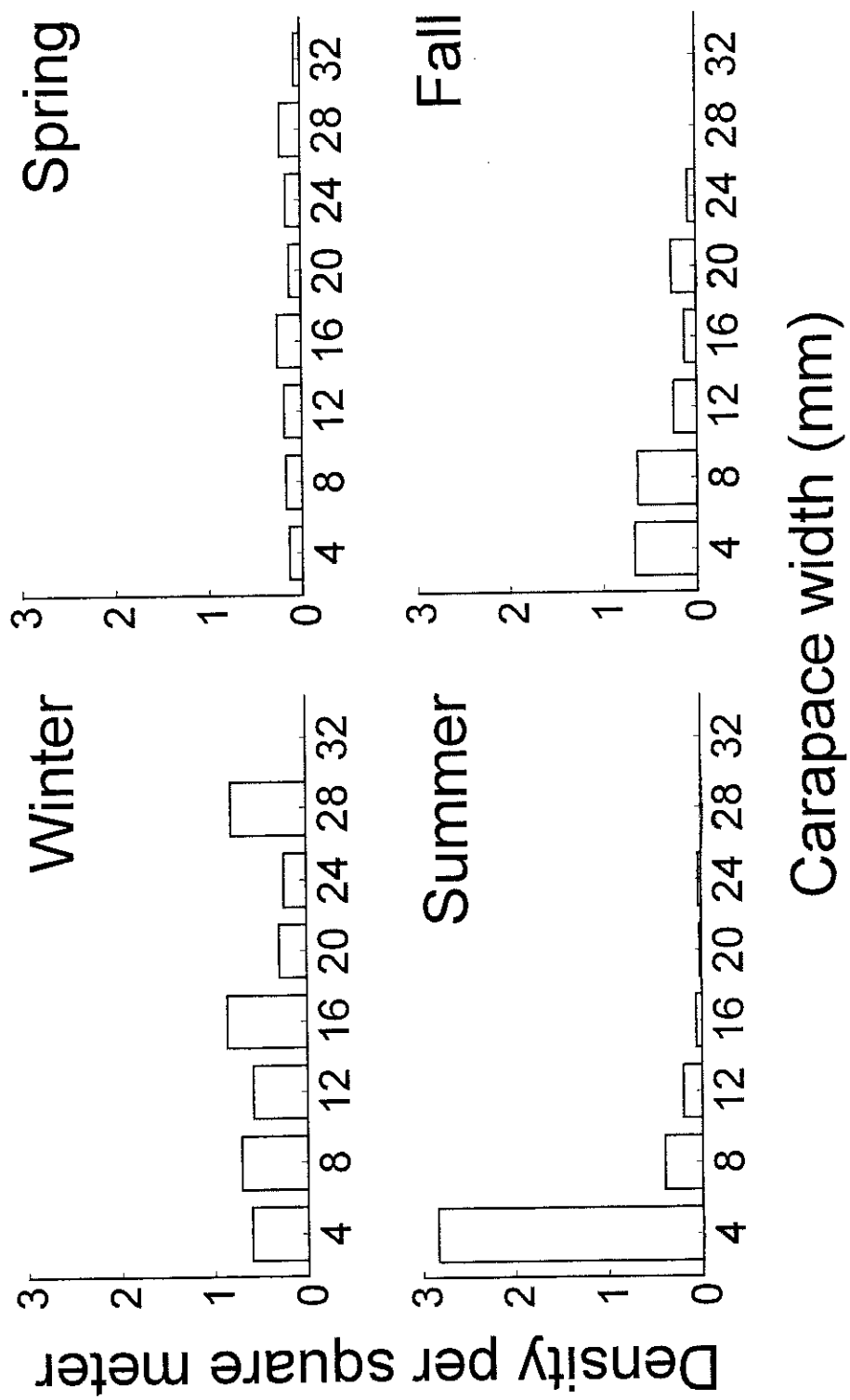


Figure 3. Size-frequency versus mean density per square meter by season for *Callinectes sapidus*.

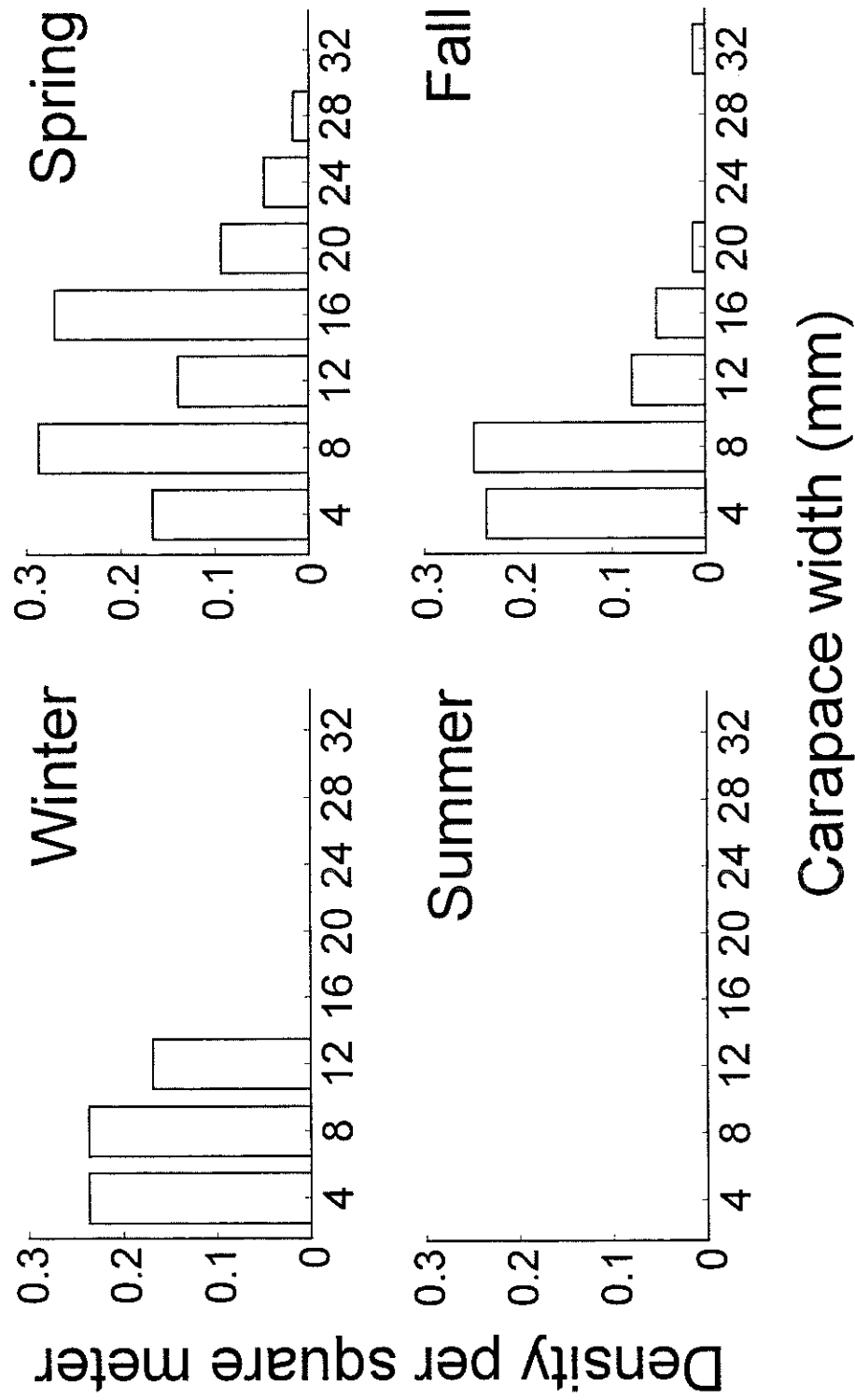


Figure 4. Size-frequency versus mean density per square meter by season for *Callinectes similis*.

Among the resident species, *Palaemonetes* spp. showed a much higher mean density in the winter; however, the total number of individuals caught did not vary much through the other seasons (Fig. 5). The higher winter density in the marsh-edge ecotone may have been caused by the low-water conditions. Grass shrimp were apparently concentrated into the tidal creeks and along the marsh edge by wind forcing that reduced marsh flooding, resulting in higher winter abundance estimates. The overall low density of small size classes in my data does not suggest a peak season of recruitment.

The hermit crab, *Clibanarius vittatus*, showed a winter recruitment peak (Fig. 6); however, the total number of individuals caught indicated fewer occurrences than in other seasons. The mud crab, *Eurypanopeus depressus*, showed a low overall density, but a distinct recruitment peak of the 3 mm size class in the summer (Fig. 7). Finally, *Mysidopsis* spp. showed an explosive increase of all size classes during the spring followed by a decrease in the other seasons (Fig. 8).

The use of available environmental space, characterized by nine environmental variables, differed significantly among the same ten species of marsh-edge invertebrates (Table 4). Because of seasonal differences in the environmental variables (Table 2), many microhabitat use patterns were undoubtedly influenced by seasonal

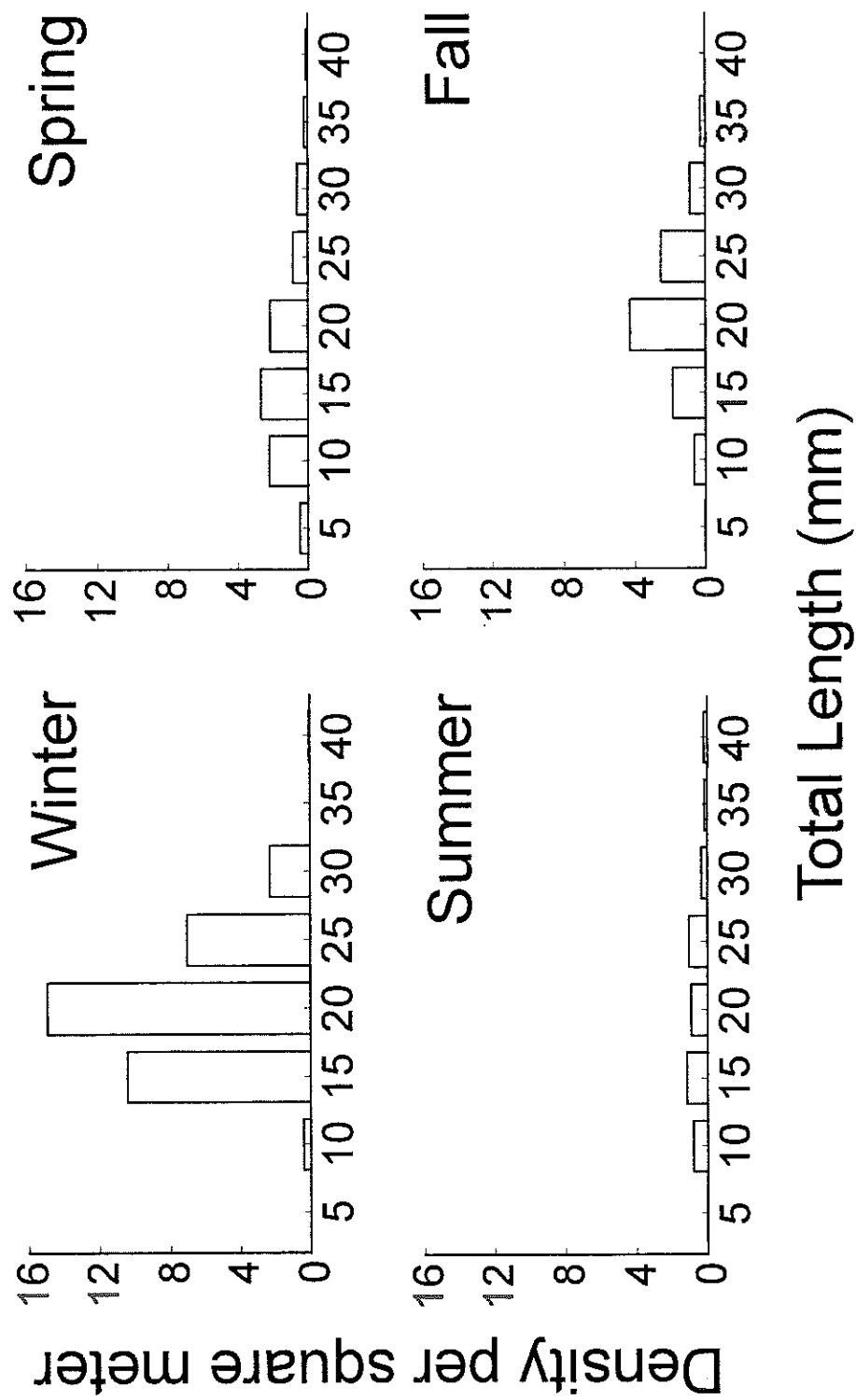


Figure 5. Size-frequency versus mean density per square meter by season for *Palaemonetes* spp.

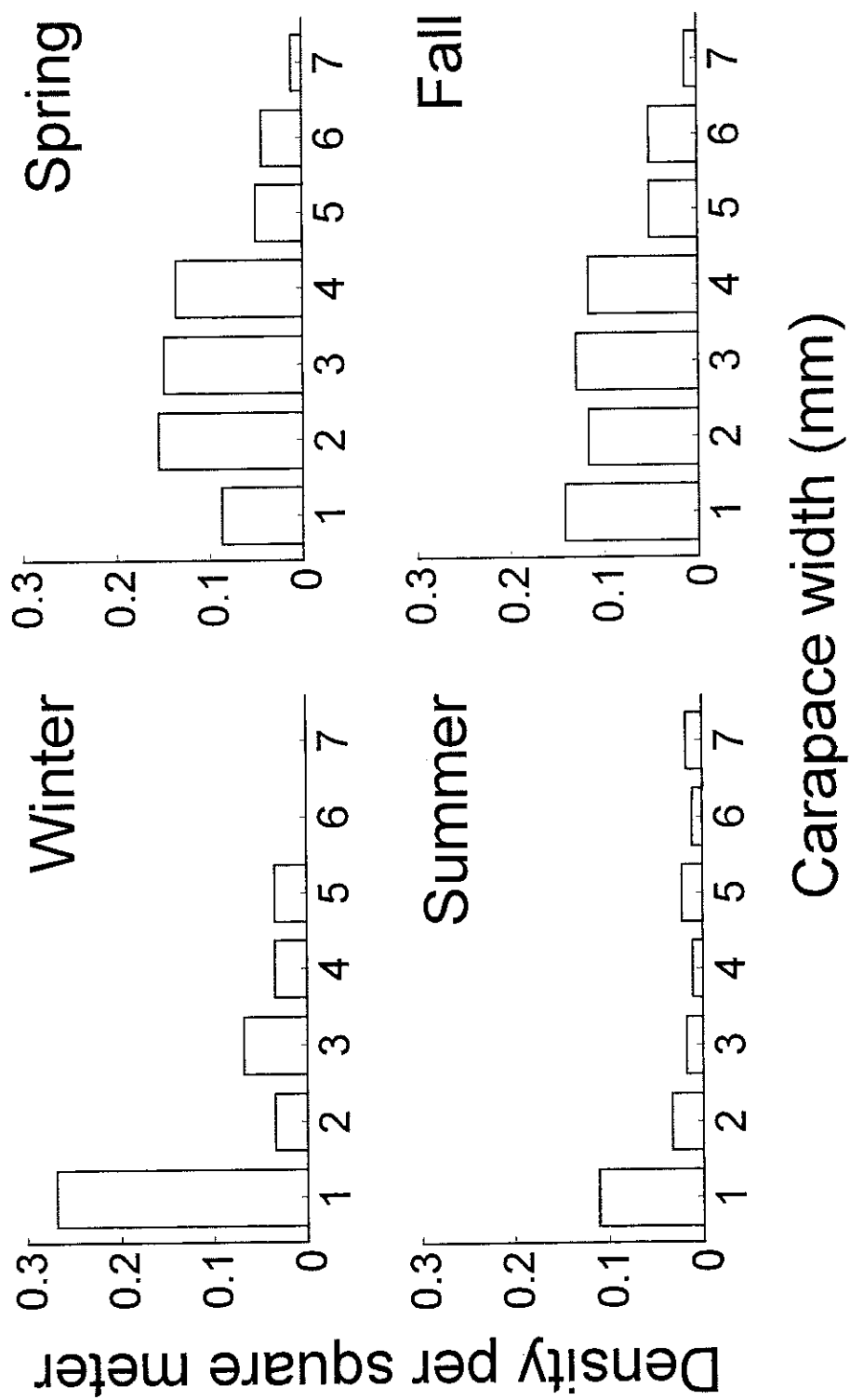


Figure 6. Size-frequency versus mean density per square meter by season for *Clibanarius vittatus*.

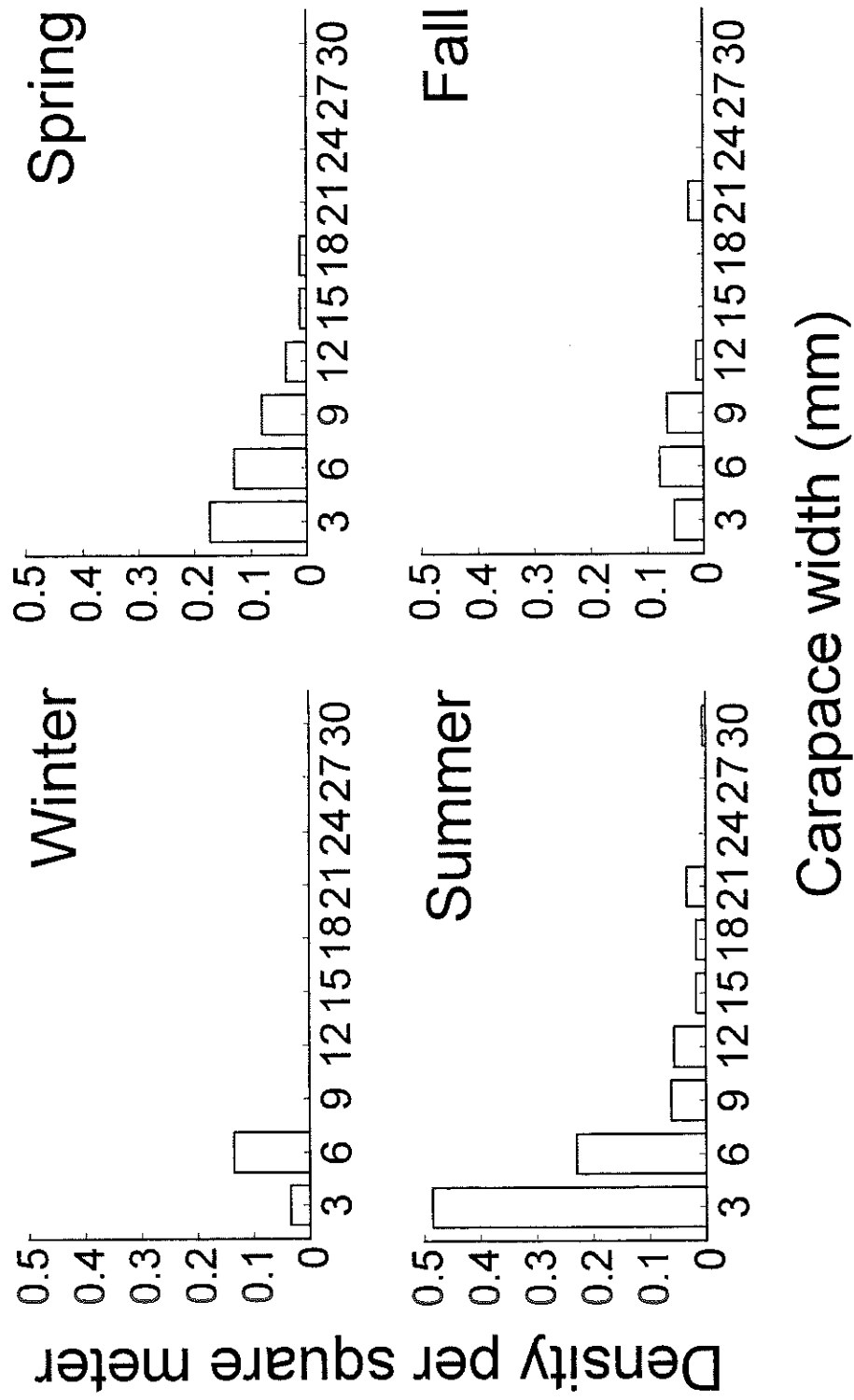


Figure 7. Size-frequency versus mean density per square meter by season for *Eurypanopeus depressus*.

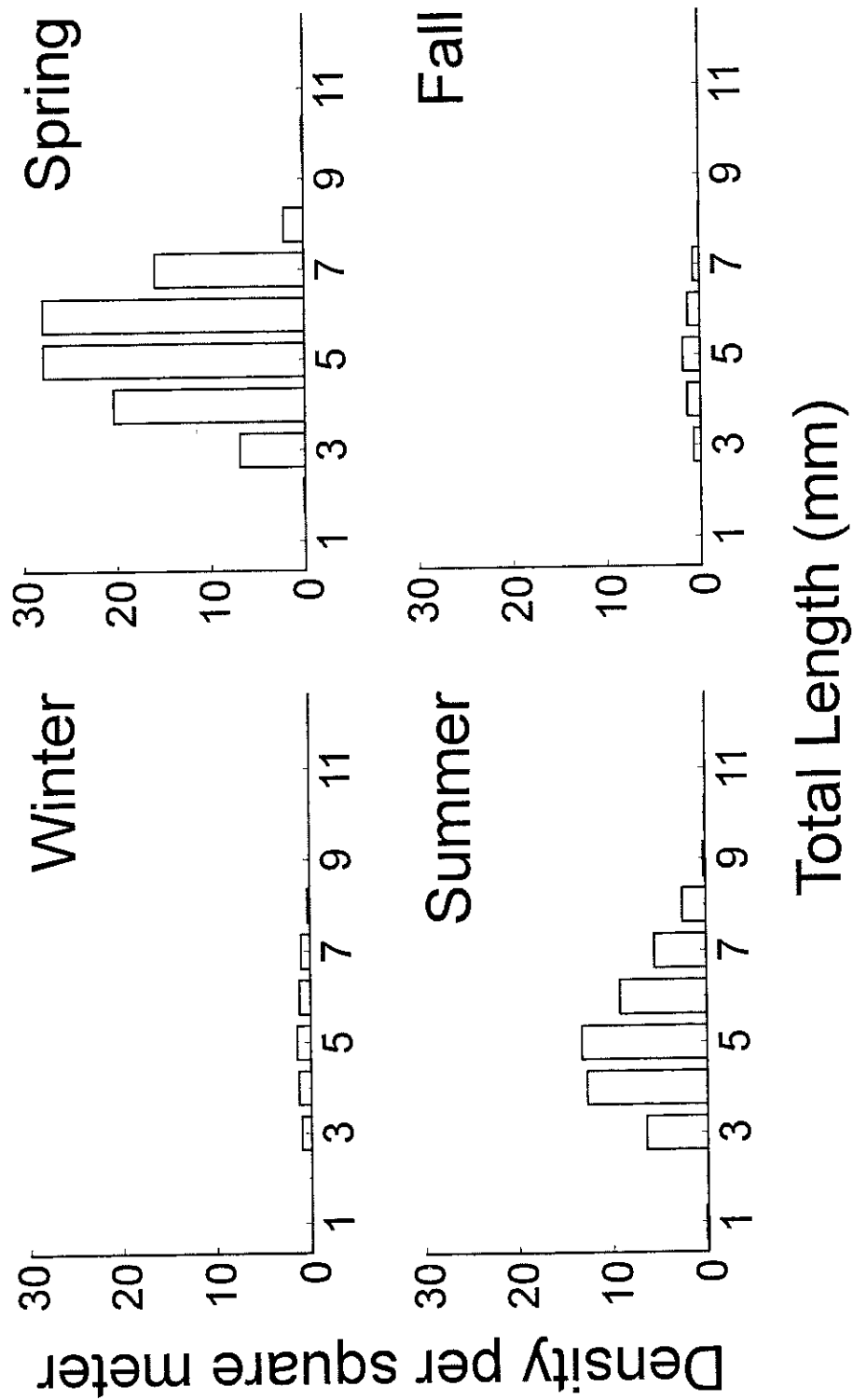


Figure 8. Size-frequency versus mean density per square meter by season for *Mysidopsis* spp.

Table 4. Means \pm 1 SE of microhabitat measurements for the ten most frequently occurring species of marsh-edge invertebrates in the Barataria Basin, Louisiana. N is number of independent observations per species. The letters, read vertically, show significant differences (Scheffe's test, $p < 0.05$) among species, within the resident or transient groups for use of a particular microhabitat variable.

Species	N	Temp. (°C)	D.O. (mg l ⁻¹)	Water depth (cm)	Dist. from edge (m)	Stems m ⁻²	Sal. (o/oo)	Vel. (cm s ⁻¹)	Turb. (NTU)	Subst. Code
Resident										
<i>Palaemonetes</i> <i>spp.</i>	241	25.6 \pm 0.34A	7.4 \pm 0.08	35.4 \pm 0.78A	1.4 \pm 0.10	12.9 \pm 1.93A	16.8 \pm 0.26	3.2 \pm 0.22	18.5 \pm 0.83	1.9 \pm 0.06
<i>Mysidopsis</i> <i>spp.</i>	233	27.5 \pm 0.28B	7.1 \pm 0.09	42.7 \pm 0.86B	1.7 \pm 0.11	4.4 \pm 0.85B	16.6 \pm 0.28	3.3 \pm 0.25	18.6 \pm 1.53	1.7 \pm 0.06
<i>Gammarus</i> <i>mucronatus</i>	105	25.5 \pm 0.49AB	7.4 \pm 0.12	38.5 \pm 1.34AB	1.2 \pm 0.14	10.9 \pm 3.67AB	16.3 \pm 0.30	3.4 \pm 0.32	18.5 \pm 1.34	2.0 \pm 0.10
<i>Clibanarius</i> <i>vittatus</i>	94	26.8 \pm 0.47AB	7.3 \pm 0.13	38.8 \pm 1.39AB	1.6 \pm 0.17	5.2 \pm 1.13AB	17.5 \pm 0.49	3.6 \pm 0.36	19.0 \pm 1.53	2.0 \pm 0.09
<i>Neanthes</i> <i>succinea</i>	93	25.2 \pm 0.56A	7.6 \pm 0.13	39.6 \pm 1.33AB	1.4 \pm 0.15	2.4 \pm 0.85B	16.6 \pm 0.43	3.7 \pm 0.39	16.2 \pm 1.14	2.0 \pm 0.10
<i>Ampileasca</i> <i>vadorum</i>	83	25.4 \pm 0.62AB	7.1 \pm 0.15	41.2 \pm 1.45AB	1.6 \pm 0.17	3.3 \pm 1.18AB	16.9 \pm 0.40	3.5 \pm 0.48	19.0 \pm 1.35	1.5 \pm 0.10
<i>Eurypanopeus</i> <i>depressus</i>	78	27.3 \pm 0.46AB	7.2 \pm 0.13	41.7 \pm 1.62B	1.5 \pm 0.17	7.7 \pm 3.45AB	15.8 \pm 0.58	3.2 \pm 0.48	17.1 \pm 1.22	1.9 \pm 0.10
(table con'd.)										

recruitment peaks. The patterns of microhabitat use showed more significant differences among the transient species than they did for the resident taxa. This may reflect differences in season of recruitment by each member of the transient group, and the accompanying seasonal changes in physicochemical variables. For all of the univariate ANOVAs, significance ($p < 0.05$) is indicated on the tables by Scheffe's test indicating a difference in means. No significant differences occurred where the Scheffe's test showed no difference, and Scheffe's test will not show differences if the ANOVA was significant.

Among the resident taxa, *Palaemonetes* spp. were found in shallower water than were *Mysidopsis* spp. or *Eurypanopeus depressus*. *Palaemonetes* were also found in higher stem densities and than *Mysidopsis*, and in cooler water, this last tendency may have been influenced by *Palaemonetes*' winter peak of abundance.

Differences in microhabitat use among transient species were more clearly demarcated, especially in regard to seasonal variables. All three transients used significantly different temperatures. *Penaeus aztecus* was found in significantly warmer water than both *Callinectes sapidus* and *C. similis*. Between the two congeners *C. similis* was found in significantly cooler water than *C. sapidus*. This tendency may have been induced or influenced by the fact that *C. similis* was not found in the summer.

Both *Callinectes* species were found in higher dissolved oxygen concentrations than was *P. aztecus*. *C. sapidus* was found in much higher stem densities than its congener and in significantly lower salinity. This lower salinity may explain the apparent absence of *C. similis* in the marsh edge in summer (Table 3, Fig. 6), when the lowest mean salinity occurred (Table 2). Also, among the three common transients, *C. sapidus* was found in significantly lower turbidity than both *C. similis* and *P. aztecus*.

In the factor analysis of the environmental variables, four factors that had eigenvalues greater than one explained 66.1% of the variance in the system (Table 5). Factor One explained 19.4% of the variance and loaded heavily for dissolved oxygen and temperature, which were negatively correlated. Thus Factor One was interpreted as a seasonal gradient, suggested primarily by the variability in temperature. The negative correlation is confirmed by seasonally significant variation of both of variables (Table 2). Factor Two explained 18.7% of the variance and loaded heavily for water depth and distance from the marsh edge, which were positively correlated. Factor Two also loaded for stem density and was negatively correlated with both water depth and distance from the marsh edge. Factor Two was interpreted as a microspatial gradient. As distance from the marsh edge increased, water depth increased and stem density decreased. Factor Three, which

Table 5. Factor analysis (with varimax rotation) of the eight variables describing environmental variation near the marsh edge. Major variable loadings (≥ 0.50) in each factor are underlined.

	FACTOR 1	FACTOR 2	FACTOR 3	FACTOR 4
Temperature	<u>-0.787</u>	0.073	-0.345	0.017
Dissolved O ₂	<u>0.828</u>	0.128	-0.176	-0.019
Depth	-0.048	<u>0.694</u>	-0.458	-0.051
Distance	-0.020	<u>0.677</u>	0.432	-0.202
Stem Density	-0.105	<u>-0.623</u>	0.044	-0.206
Salinity	0.048	<u>-0.038</u>	<u>0.879</u>	0.024
Velocity	0.194	0.128	-0.064	<u>0.721</u>
Turbidity	-0.281	-0.074	0.082	<u>0.738</u>
Variance Explained	1.552	1.500	1.137	1.105
Proportion Explained	0.194	0.187	0.142	0.138
Cumulative Proportion	0.194	0.381	0.523	0.661

explained 14.2% of the variance and loaded heavily only for salinity, was interpreted primarily as a macrospatial salinity gradient along the lower, middle, and upper reaches of the transects. Finally, Factor Four explained 13.8% of the variance and loaded heavily for velocity and turbidity, which were positively correlated. Factor Four was interpreted as a weather and tide related axis. As water velocity increased, the resuspension of fine substrate material increased the turbidity. Factor analysis only explains two-thirds of the variance within this system. Although Factor One was interpreted as a seasonal gradient, other factors may also have included some seasonal components of variation which were reduced by rotation. For example, the seasonal analysis of environmental variables (Table 2) showed that salinity (Factor Three) had a strong seasonal component, as did turbidity and water velocity (Factor Four).

In the plot of frequently occurring species in three-dimensional environmental space (Fig. 9), several species (i.e., *Mysidopsis*, *Gammarus mucronatus*, *Ampliesca vadorum*, and *Palaemonetes*) showed a wide distribution while other species were more narrowly confined, especially *Penaeus aztecus*, *Callinectes sapidus*, *Clibanarius vittatus*, and *C. similis*. The one-standard-error balloons around species' centroids for certain species do not overlap; however, tests of differences between species, indicated by non-

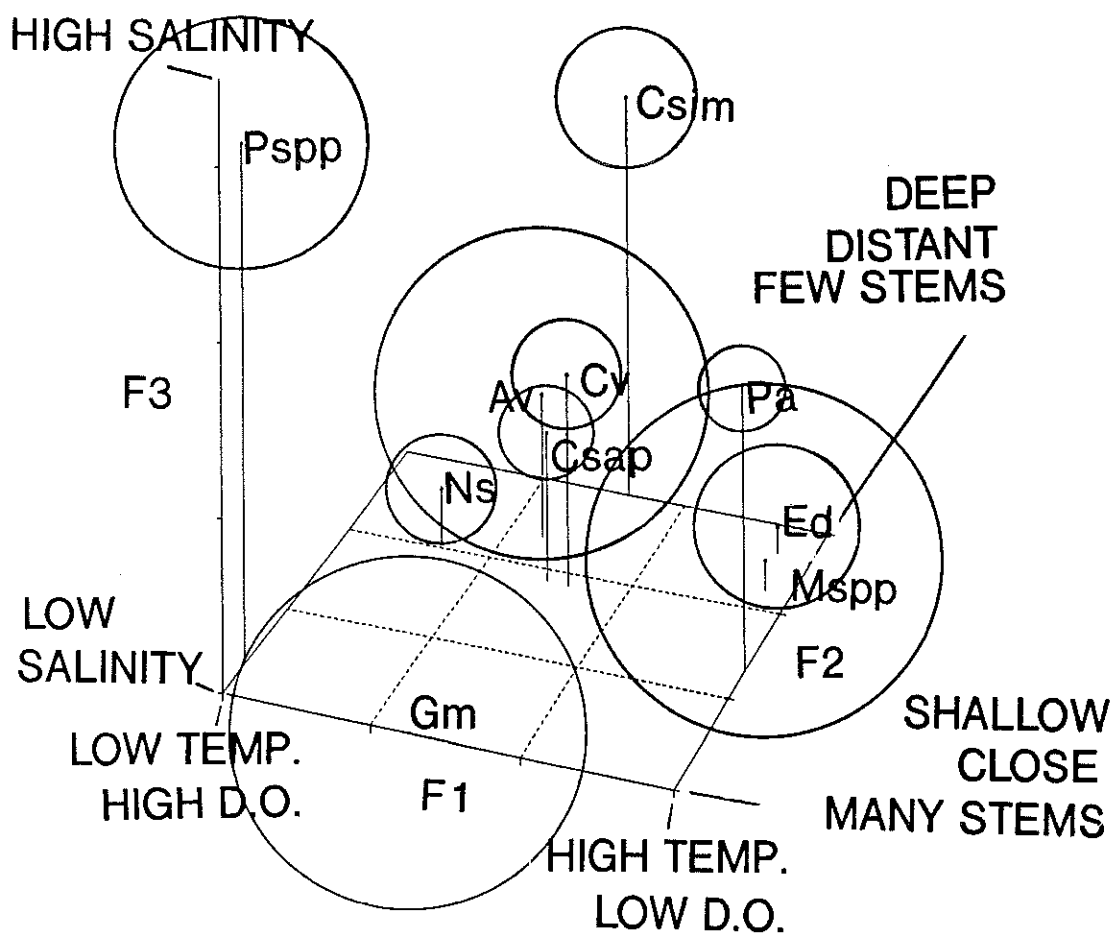


Figure 9. Plot of the factor analysis of the ten most commonly occurring macroinvertebrates in the marsh edge.

overlap of two standard errors, showed that *C. sapidus* were significantly different from *C. similis*, especially along the Factor Three axis which is the macrospatial or salinity gradient. *Palaemonetes* were found in significantly higher salinities than even *C. similis*. *Palaemonetes* was significantly different from all species, except the widely ranging *A. vadorum*, in its use of environmental space at the extremes of both the Factor One and Factor Two axes. *Penaeus aztecus* and *Eurypanopeus depressus* used lower temperatures, and, except for the more eurythermal *Mysidopsis*, formed a species pair at the far end of the Factor One axis. Although not significantly different, there was also an apparent gradation of amphipods from *G. mucronatus* in shallow water to *A. vadorum* in deeper water.

Discussion

In this study we have demonstrated that there was differential use of the marsh-edge ecotone by some of the most frequently occurring macroinvertebrates. Some of these microhabitat differences are due to seasonal patterns of abundance, and are related to the season of recruitment within the estuary. Also, the occurrence of mostly smaller size classes for certain species in the marsh edge is a confirmation of its importance as a nursery ground.

Given the limits of this study, it is impossible to say if these species show the described use patterns because they are taken at different seasons, or if they are taken at different seasons because they have evolved to tolerate different environmental conditions. As Connell (1980) pointed out, this sort of question is tautological, and ultimately untestable except over evolutionary time scales.

In considering gear selectivity, it is unlikely that many invertebrates could have avoided the sampler, as a quiet approach was used to reduce startling organisms and turbidity greatly reduced the chance of visual avoidance. In the course of this study many fishes were caught including several large red drum, *Sciaenops ocellatus*, measuring up to 44 cm in total length. Since fishes are more mobile organisms than most invertebrates, the chance of escape by macroinvertebrates was negligible. In general the abundances of macroinvertebrates were representative except for burrowing or tube-dwelling species. Among the ten most frequently occurring taxa, this would include *Gammarus mucronatus*, *Ampileasca vadorum*, and *Neanthes succinea*. For these three species, the sampling methods used probably underestimated the actual abundances.

The macroinvertebrate assemblage along the marsh edge was numerically dominated by four resident taxa and one transient species. *Mysidopsis*, *Palaemonetes*, and two

amphipods (*G. mucronatus* and *A. vadorum*) were the residents and *Callinectes sapidus* was the transient. Together these taxa accounted for 92% of all individuals. sampled.

The assemblage composition changed seasonally because of recruitment to the marsh edge by early life history stages, particularly of transient species. Analyses of several temporally and spatially influenced microhabitat use variables indicated that segregation between resident taxa was more limited than for transient species, especially when looking at seasonally influenced variables. One might think this to be counterintuitive; however, a transient species or life-history stage is more likely to have a narrower range of environmental tolerance than a species that lives year-round in an estuary. Temperature, water depth, and stem density were the variables that contributed most significant differences among resident taxa. Several temperature differences were probably strongly influenced by seasons of recruitment. Magnuson, et al. (1979) suggested that temperature was as much an ecologic resource as food, and that temperature and other niche axes should be viewed in that manner. Temperature showed even more significant differences between the transient species, emphasizing their seasonal recruitment pulses. Other significant variables were dissolved oxygen, stem density, salinity, and turbidity. Baltz et al. (1992) found significant temporal and spatial segregation within

several ecological groups of fishes, including both residents and transients. Their study, however, focused on several life history stages of each fish they examined. More differences between resident macroinvertebrates might have been delineated in this study if the analyses included an examination of size classes.

Due to gear limitations of seines and trawls, most previous studies of estuarine macroinvertebrates focused on large juveniles and adults in open water. Our drop sampler quantified the abundant small and early life-history stages of estuarine macroinvertebrates that use the marsh-edge ecotone. This approach allowed examination of microspatial, as well as large-scale salinity gradients in species distributions and community structure. In addition, a clearer picture of recruitment patterns within the marsh edge ecotone was obtained.

Patterns in the community structure of marsh-edge invertebrates involving different species associations were clarified by plotting the factor scores of each species against the three-dimensional axis of seasonality, salinity, and microspatial variation (Fig. 9). This plot summarized the complex multidimensionality of the system, and indicated the influence of complex gradients. Since the estuaries of the northern Gulf of Mexico are a large fraction of remaining of coastal wetlands in the United States, it is important to know that a gradient model can

be applied to the analysis of their invertebrate fauna. *Penaeus aztecus* showed a spring peak in the recruitment of size classes ranging from 10 to 80 mm into the marsh edge. This corresponded with the traditional pattern of winter or early spring spawning in offshore waters over the continental shelf (Cook and Linder 1970) and then subsequent entry into the bays in large numbers throughout spring. These small (10-15mm, total length) brown shrimp have been reported to migrate to shallow and often vegetated nursery areas (Baxter and Renfro 1967, Zimmerman et al. 1984). The reduction in smaller size classes through the summer may have been through growth to larger size classes, migration away from the marsh edge, or due to mortality. Minello et al. (1989) found that mortality may be the ultimate control over the brown shrimp population, particularly through predation by the southern flounder, *Paralichthys lethostigma*. Disappearance of the larger size classes in fall may be due to movement into deeper waters. Baxter et al. (1988) reported that juveniles over 55-66 mm TL move into the open bays and become susceptible to the fishery.

Callinectes sapidus displayed a clear recruitment peak in the marsh edge during summer. In the Gulf of Mexico, small juvenile blue crabs have been reported in the estuary throughout the year; however, there is considerable variation in abundance and spawning seasons (Daud 1979,

Rogers and Herke 1985, Thomas et al. 1990, Williams et al. 1990). More (1969) reported catches of egg-bearing females during mild winters and speculated that spawning occurred year round. Recruits to the estuary may occur the year round, but the smallest juvenile crabs seemed to congregate in shallow water or in stems. This is reinforced by Thomas et al. (1990) who found that densities of juvenile blue crabs were highest in seagrass beds, followed by submerged *Spartina*, and then bare sand. Living close to the marsh edge, juvenile blue crabs would have relatively easy access to flooded *Spartina*, and they would find some protection from large aquatic predators who avoid shallow water. The sampling technique that we used focused on the marsh-edge ecotone, and this may have resulted in seeing the recruitment peak in summer. Gibson (1991), also working in the marsh-edge ecotone, reported the highest densities of blue crabs occurred in the month of August.

Published data are lacking on *Callinectes similis*. Juveniles and adults have been reported in Gulf of Mexico waters (Rozas and Odum 1987), but little work has been done with them save by Williams (1985) and Gibson (1991). Gibson's samples were taken from this sampling program; however, the time frames of our studies did not exactly coincide. Gibson found peak abundances of *C. similis* in August, which does not correspond with my own observation. I found no *C. similis* present in the marsh edge during the

summer months. It is possible that spawning peak which Gibson reported as being in June and July resulting in an August recruitment, was late or delayed during the year of my sampling. Gibson sampled from December 1989 through January 1991, while this study was from August 1988 through September 1989. Gibson's findings generally agreed with Stuck and Perry (1981) and Perry and Stuck (1982) who reported a winter spawning peak and a smaller summer spawning peak based on the presence of megalopae in the Mississippi River. These results may differ from Gibson's because the summer samples from this study were taken during the 1987-1988 La Niña event (Childers et al. 1990).

As was mentioned in the results, northerly winds often cause low-water conditions within the estuary during the winter months. This low-water condition is normal; however, the extremely low-water levels seen during the winter of this study were probably due to climatological forcing from the 1987-1988 La Niña event (Childers et al. 1990). This may have influenced many factors in this study as the marsh was not flooded at all for several weeks.

As to the occurrence of *Callinectes similis* in higher salinity water than *C. sapidus* as detailed by the factor analysis (Fig. 9). While there is some seasonal variation in salinity, this difference confirms the observation that *C. similis* is more abundant in the lower reaches of the study area (Gibson 1991).

The large numbers of adult *Palaemonetes* spp. in winter are difficult to explain. It has been noted that juvenile *Palaemonetes* remain on the flooded marsh surface while adults congregate at the marsh edge or in tidal creeks (Knieb 1987). Knieb was not able to discover the causative factors for this; however, he suggested that segregation might reduce competition between adults and juveniles and perhaps serve as a mechanism to prevent predation on the juveniles by adults. Also, it is possible that the low-water conditions for this winter concentrated *Palaemonetes* in the shallows as they were forced away from the marsh surface.

Having described some of the microhabitat use patterns of common organisms within this system, the next logical step is experimentation. Describing the environmental conditions under which a species or life history stage is found in does not confirm the species full environmental tolerance range, nor does it answer the question of environmental preferences. Experiments could be devised to learn what the preferences of these organisms are. Also, experiments can be conducted to see if there is some other factor that influences microhabitat selection, such as competition with other organisms, higher densities of prey organisms, or predator avoidance.

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CHAPTER 3

PREDATION ON SMALL FISH NEAR THE MARSH EDGE

According to the 'nearest refuge' hypothesis of Virnstein and Curran (1986), emigration from vegetation, for whatever reason, should be nocturnal to avoid the expected higher predation risk in unvegetated areas during the day (Orth 1992). Zimmerman et al. (1989) proposed the hypothesis that the marsh-edge ecotone is used by fishes as a corridor between the marsh habitats and open water. The importance of this 'corridor' has been examined in detail in recent studies (Baltz et al. 1993). To test this hypothesis, tethering experiments were conducted over unvegetated substrates at the marsh edge, to determine if there was differential survival between day and night on fish moving through unsheltered areas while seeking refugia (i.e., during the process of microhabitat selection).

The predation experiments were conducted using the technique of chronographic tethering developed by Minello et al. (1993). The digital timers used for the experiments were Trail Timers® (Trail Timer, St. Paul, MN) normally used for measuring animal movement events (Fig. 10). The timers were attached to a highline made of heavy (25 lb. test) fishing line supported above the water by 2 m long bamboo poles. The poles were planted 50 cm into the sediment, giving the highline about 1 m of clearance above the high tide mark. The timers were spaced along the highlines at 3 m intervals, ensuring that there was an adequate distance between individual prey to avoid tangling

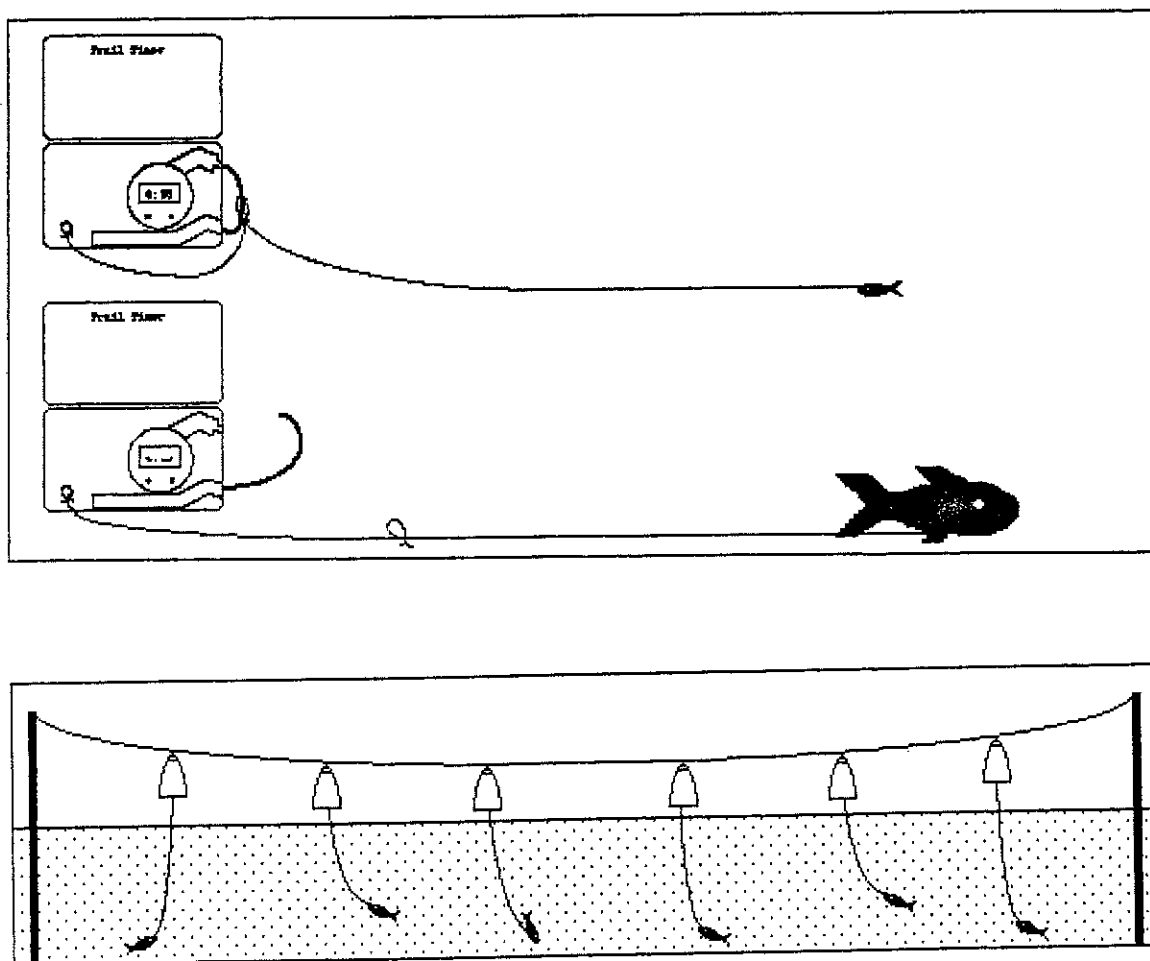


Figure 10. Diagram of the chronographic tethering technique.

of tethers with other prey, and to limit repeat-feeding by one predator along the highline. Four separate highlines with six timers each were placed near the marsh edge in different locations within a shallow bay near LUMCON (Fig. 11). Each highline was located within 1.5 m of the shore in approximately 50 cm of water. Each timer was covered by an inverted plastic cup to protect it against moisture damage from precipitation.

For this experiment we used gulf killifish (*Fundulus grandis*) as the prey species. The prey were attached to the timer by 1 lb. test monofilament fishing leader threaded through the mouth and gill opening. These lines were secured with a knot that would not tighten down on the fish. The tethers were attached through the timer trigger and again to the clip that secured it to the highline. The secondary attachment was to be certain that if the prey managed to trigger the timer by itself, it could not escape, and thus it would not be inaccurately reported as predation event. It was impossible, given the limits of this study, to deal with the possibility of a prey triggering the timer itself, then being eaten at a later time.

Prey animals were set out on four occasions, two day samples and two night samples. To differentiate the effects of night versus day, the prey were set after dawn and retrieved before dusk in the day samples, and set after

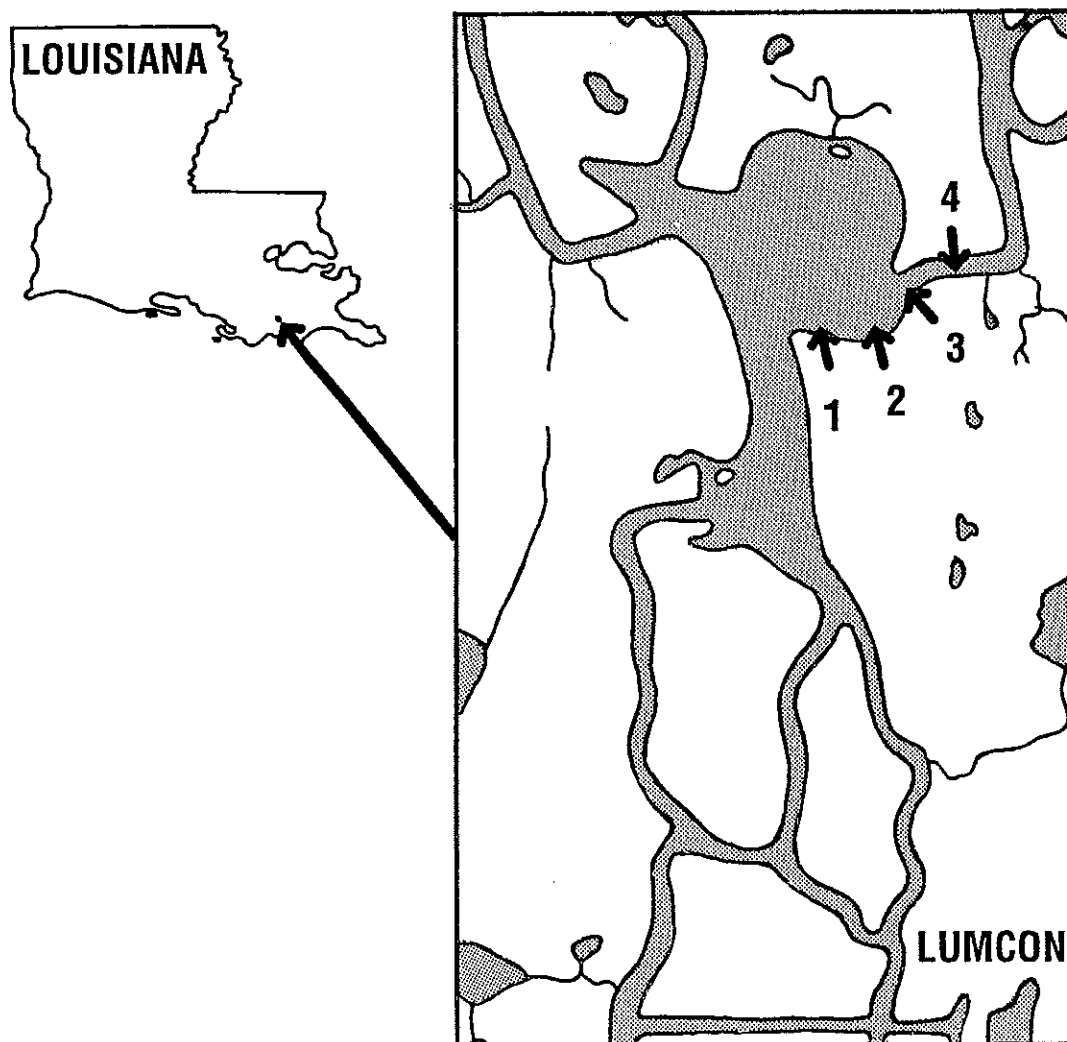


Figure 11. Map of the LUMCON region, numbers indicate the sites where tethering highlines were set.

dusk and retrieved before dawn for night samples. When a timer was triggered, and the fish on the tether was gone, this was recorded as a predation event. Occasionally a timer was triggered, and the prey item was still on the line. Whereas this might represent a near predation event (the prey escaped the predator, but in so doing triggered the timer), it was still counted as a non-predation event and excluded from the data analysis. For all predation events, the trigger time was recorded and used to calculate the survival time (in minutes) of each prey (Table 6). Those prey not taken by a predator had a truncated survival time which equaled the duration of the experiment. None of the fish were reused in later trials, and the total length of each fish was taken to assess the effects of prey size as a covariable. Other environmental measurements were taken after each complete set of six prey animals had been emplaced, including water temperature, salinity, turbidity, and dissolved oxygen.

Ranked survival times were used because the distributions were truncated and violated the assumption of normality. The data were analyzed using a two-way analysis of variance with interaction between time and station on the ranked survival times. The analysis was run using the general linear model procedure in the SAS program package (SAS Institute 1985). The results were interpreted using model-order-independent sums of squares.

Table 6. Summary statistics for the survival times for 96 prey animals set out in a day-versus-night experiment at four different stations near the LUMCON research facility.

	N	Min.	Max.	Mean	Std.Dev.
Time					
Day	41	14	809	505.4	293.92
Night	45	48	902	445.9	242.53
Station					
1	24	14	729	440.4	225.12
2	22	48	902	501.8	311.58
3	20	221	804	579.8	181.36
4	20	68	809	379.3	282.05

The analysis of ranked survival times showed significant interaction effects ($p < 0.002$) between time (i.e., day versus night) and station (i.e., the four locations). Because one of the highlines (Station 4) was strung near the mouth of a tidal creek, this may have resulted in a significant station effect ($p < 0.043$) resulting in the interaction. There was also a significant day versus night effect ($p < 0.022$) with a lower mean survival time during the day (Table 6). In the plot of mean survival time of the tethered fish for day versus night at the four stations (Fig. 12), using two standard errors as a visual test of differences, it can be seen that daytime survival was significantly lower than nighttime survival at two of the four stations. It is possible that all the sites were not selected to be similar enough to reduce the effect on a statistical analysis.

The strong interaction between time and station does not allow reduction of the model, and suggests that reconstruction of this experiment should focus on selecting sites that have fewer differences between them.

Unexpectedly strong effects were observed because one station was located near a creek mouth. The data were reanalyzed, excluding station 4 at the tidal creek, and it resulted in no significant effects between stations, or between day and night. This could suggest that most of the predation activity that occurs near the marsh edge is

associated with major marsh features such as tidal creek mouths. It could also suggest that the experiment was not sensitive enough to detect predation effects except in a place where large predators can congregate near the shallows such as a tidal creek. However, even with this removal, there was still a significantly lower daytime survival at Station 3 (Fig. 12).

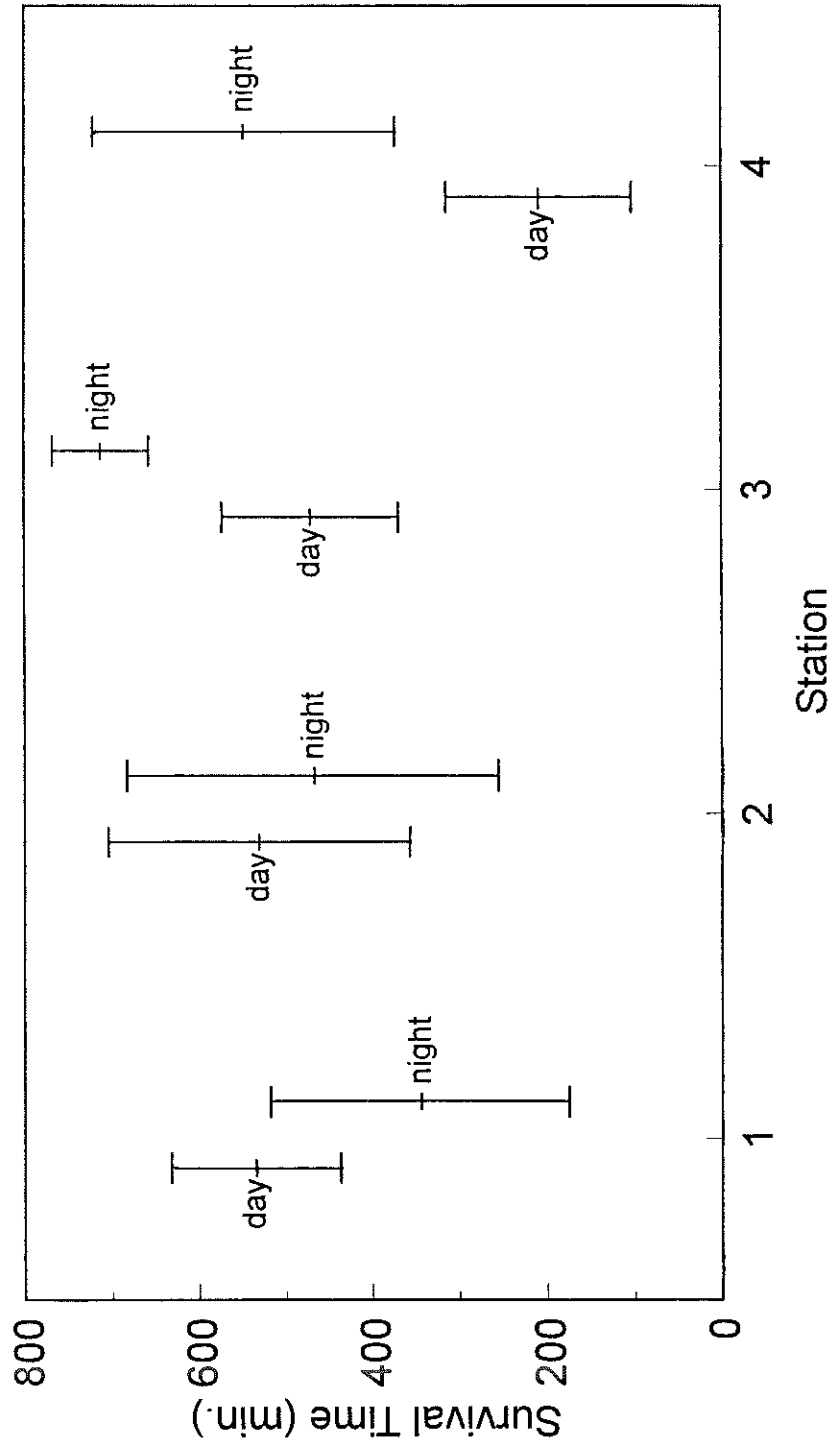


Figure 12. Mean survival time in minutes (+ 2 SE) of tethered *Fundulus grandis* at four different stations near LUMCON during the day and night hours.

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CHAPTER 4

SUMMARY AND CONCLUSIONS

In this study the marsh-edge ecotone of the Barataria Basin has been sampled for macroinvertebrates. Factor analysis was used to identify the important gradients within the estuarine system, and to model the seasonal, microhabitat, and macrogradient use of invertebrate taxa in the lower estuary. General linear models were used to elucidate each of the major species-use patterns for specific environmental variables. Size-frequency analysis was used to show seasonal patterns of recruitment.

The major axes influencing community structure in the Barataria Basin include a temporal change of temperature and dissolved oxygen (a seasonal response), salinity (a large-scale spatial response), and microspatial variation in depth, distance, and stem density. The macroinvertebrate taxa arrayed themselves differentially along these axes. The temperature gradient reflected greater differences among transient species in the estuary than among resident taxa.

Drop sampling gives good estimates of macroinvertebrate abundance in the marsh-edge environments. This method could serve to clarify the environmental requirements of many fishes and macroinvertebrate species. The results of this study give us a better understanding of the microhabitat use patterns of several macroinvertebrates, and thus a greater understanding of what constitutes their ecological requirements.

Through this methodology we have shown that the marsh-edge ecotone in the Barataria Basin may be an important nursery area for many macroinvertebrate species.

The technique of chronographic tethering is a promising method for conducting small scale predation experiments. In this study problems arose in analyzing the data parametrically because of the truncated distribution which resulted from incomplete predation during the experiment's time interval. However, the study produced some evidence that daytime survival rates are lower than those at night in the marsh-edge ecotone.

VITA

William Harold Francis Hayden was born on November 10, 1960 in Livermore, California. He attended grammar school and high school in Livermore which is an inland city. It was on family trips to Half Moon Bay, and the Monterey Coast that he was exposed to the rocky intertidal, and developed his initial interest in the marine sciences. His family moved to the Los Angeles area in 1975, and he attended his last two years of high school at Westchester High School where he graduated in 1977. His family's new home was in Playa del Rey, just five blocks from the beach, and three blocks from the Cabrillo Wetlands. He attended the University of Southern California in the hope of taking a semester of studies at the Catalina Marine Science Station maintained by USC. In his last semester he fulfilled that hope, and completed undergraduate degree in Zoology in 1981. After college he worked for two years, trying to repay some college loans and save money for graduate school. Prior to applying for advanced studies he traveled cross-country with his brother to see more of the United States. Visiting Louisiana, he was impressed with the vast wetlands, the like of which he had not seen in California. He initially applied for graduate studies at Moss Landing Marine Laboratories in 1985. Working part time at the marine lab as a library assistant, a teaching

assistant, and training students to operate the Microvax computer, he slowly worked toward his Master of Science Degree in the Marine Sciences. In 1989, the Moss Landing Marine Laboratory was devastated by an earthquake, and he decided to complete his degree program at another institution. Holding his research for later completion and publication, he applied and was accepted as a graduate assistant, and a candidate for an advanced degree at Louisiana State University and Agricultural and Mechanical College. He will graduate in August 1994 with a Master's degree from the Department of Oceanography and Coastal Sciences, and a minor from the Department of Experimental Statistics.

MASTER'S EXAMINATION AND THESIS REPORT

Candidate: William H. F. Hayden

Major Field: Oceanography and Coastal Sciences


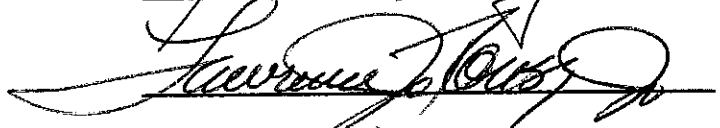

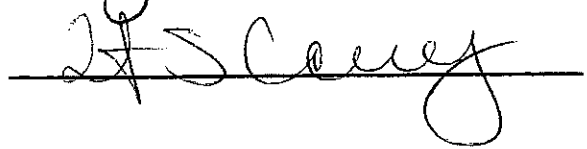
Title of Thesis: Microhabitat Use by Macroinvertebrates in
Barataria Bay, Louisiana

Approved:


Major Professor and Chairman


Dean of the Graduate School

EXAMINING COMMITTEE:

Date of Examination:

June 30, 1994

